Nectar Robbery by Bees *Xylocopa virginica* and *Apis mellifera* Contributes to the Pollination of Rabbiteye Blueberry

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ABSTRACT   Honey bees, *Apis mellifera* L., probe for nectar from robbery slits previously made by male carpenter bees, *Xylocopa virginica* (L.), at the flowers of rabbiteye blueberry, *Vaccinium ashei* Reade. This relationship between primary nectar robbers (carpenter bees) and secondary nectar thieves (honey bees) is poorly understood but seemingly unfavorable for *V. ashei* pollination. We designed two studies to measure the impact of nectar robbers on *V. ashei* pollination. First, counting the amount of pollen on stigmas (stigmatic pollen loading) showed that nectar robbers delivered fewer blueberry tetrads per stigma after single floral visits than did our benchmark pollinator, the southeastern blueberry bee, *Habropoda laboriosa* (F.), a recognized effective pollinator of blueberries. Increasing numbers of floral visits by carpenter bee and honey bee robbers yielded larger stigmatic loads. As few as three robbery visits were equivalent to one legitimate visit by a pollen-collecting *H. laboriosa* female. More than three robbery visits per flower slightly depressed stigmatic pollen loads. In our second study, a survey of 10 commercial blueberry farms demonstrated that corolla slitting by carpenter bees (i.e., robbery) has no appreciable affect on overall *V. ashei* fruit set. Our observations demonstrate male carpenter bees are benign or even potentially beneficial floral visitors of *V. ashei*. Their robbery of blueberry flowers in the southeast may attract more honey bee pollinators to the crop.

KEY WORDS   honey bee, carpenter bee, *Vaccinium ashei*, pollination, *Habropoda laboriosa*

NECTAR ROBBERY IS A SIGNIFICANT concern for blueberry producers who rely on European honey bees, *Apis mellifera* L., for supplemental blueberry pollination. Worker honey bees are often essential for the pollination of rabbiteye blueberry, *Vaccinium ashei* Reade, because the crop's major cultivars exhibit strong genetic self-incompatibility and native bee pollinator populations sometimes dwindle to unsatisfactory levels (<1 bee per bush; Free 1970, Sampson and Cane 2000). Although honey bees often outnumber native bees at flowering bushes (R.G.D. and B.J.S., unpublished data), doubt still lingers about a honey bee's overall effectiveness as a blueberry pollinator (Payne et al. 1989, 1991; Cane 1993; Cane and Payne 1993) because workers do not actively gather blueberry pollen and they have a stronger predilection for gleaning nectar from robbery slits first cut into blossoms by carpenter bees, *Xylocopa virginica* (L.).

Flower robbery chiefly occurs from March to early April when honey bee and carpenter bee foraging populations broadly overlap (Cane and Payne 1993). Primary floral robbery commences after a carpenter bee pierces the base of the blueberry corolla to access nectar near the bottom of the pistil. Resorting to secondary floral robbery presumably gives shorter tongued honey bees easier access to nectar glands than if they had inserted their proboscides through the narrow, terminal opening of a blueberry flower. Honey bees seldom probe *V. ashei* flowers in a legitimate manner when carpenter robbery slits are readily available. As few as 4–50% flowers robbed by *Xylocopa* will incite 65–100% of honey bees to steal nectar (Delaplane and Dedej 2001, R.G.D. and B.J.S., unpublished data). Robbery visits in which the corolla opening is bypassed may result in bees failing to pollinate flowers because pollen-receptive stigmas are located at the top of the pistil and away from the robbery slits. Other putative drawbacks generally associated with floral robbery by carpenter bees and honey bees include damage to flowers and increased interspecific competition among pollinators (Pleasants 1983, Roubik 1992).

Given these seemingly negative aspects associated with nectar robbery, it was hypothesized that robbery by *Xylocopa* and *Apis* is an impediment to commercial blueberry pollination and production (Dorr and Martin 1966, Marucci 1967, Oldershaw 1970, Payne et al. 1991). However, several research articles [summarized by Maloof and Inouye (2000)] from various plant taxa recognize the potential reproductive benefits of some illegitimate floral visitation. At the flowers of lady's fingers, *Anthyllis vulneraria* L., robbery by carpenter bees increases the percentage of fruit set by 50% compared with unrobbed flowers. The few data available for *V. ashei* indicate that robbery has more subtle effects by slightly enhancing fruit set, but re-

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ducing the average number of seeds per berry (Delaplane and Dedej 2001). Thus, some illegitimate floral visitors differ from the "true" nectar robbers or thieves because they enhance rather than reduce the reproductive fitness of certain floral hosts (Roubik 1992).

Widespread nectar robbery by *X. virginica* and *A. mellifera* during *V. ashei* anthesis prompted us to directly measure the pollination efficacies (i.e., stigmatic pollen loading) of illegitimate foragers from both species. Stigmatic loading is one measure of an individual bee's pollination efficacy. It allows for a comparison between primary and secondary robbers, as well as robbers and nonrobbers, and unlike fruit set is impacted by fewer random factors such as bee density, drought, severe weather, and pests (Sampson 1993). The impact of carpenter bee robbery on commercial blueberry production was also assessed by preliminarily correlating floral robbery rates with percentage of fruit set in a group of commercial blueberry farms.

Materials and Methods

Stigmatic Pollen Loading Study. Experimental plants consisted of the standard *V. ashei* 'Climax', 'Premier', and 'Tifblue'. These plants were ≈1.25 m in height and grown in 30-liter (7-gal) pots. Four plants from each cultivar were placed in one of three cages to exclude pollinators. These 1.5 by 1.0 by 1.0-m cages were made of Lumite mesh and provided enough space for four potted blueberry plants. Caged *V. ashei* plants were placed adjacent to a 0.13-ha plot of 'Tifblue', 'Woodard', and 'Delite' bushes (pollinizers) (*n* = 150 at the USDA–ARS Small Fruit Research Station, Poplarville, MS). The pollinizer varieties were originally planted in a checkerboard pattern ≈20 yr ago. This pattern should make it possible for robbing bees to deliver a higher proportion of compatible pollen tetrads to the stigmas of our caged flowers. Stigmas were not harvested and analyzed for pollinizer bushes because they strictly served as pollen donors. Predominant floral visitors to blueberries in this plot were *X. virginica* and *A. mellifera*. Weather conditions during this study in March 2003 were optimal for bee flight: clear sky, gentle wind, and daily high temperatures from 18 to 23°C.

Cages were removed periodically to give free-flying bees access to previously unvisited 1- or 2-d-old flowers on these plants. A plant was considered as a replicated block from which flowers were plucked after being visited by a bee. The species of bee and its visitation behavior on the flower determined which of the possible seven treatment classes (see below) the flower should be assigned. All treatments were nested within bushes. Often, many treatments would occur even on the same inflorescence. A group of unvisited flowers from the same or different inflorescences were used as controls, and they accounted for any autogamy or incidental pollination that might have occurred inside cages. *X. virginica* males initially were permitted to rob unvisited flowers on potted plants that were

removed from a cage, especially for earlier blooming 'Climax'. However, foraging sequences of *X. virginica* visits followed by *A. mellifera* visits were infrequent. Therefore, we increased the percentage of robbed flowers on our caged plants, as well as corolla slitting frequency by caging two, four, and 11 field-collected *X. virginica* males with 'Premier' and 'Tifblue' plants from 800 to 1000 hours or 1100 hours (2–3 h) on three separate occasions. 'Climax' plants could not be treated in this way because they had finished blooming. Plants were removed from the cages to be visited by other bee species (mostly *A. mellifera*) after enough flowers were slit. Honey bees were extremely plentiful and when they discovered our plants, they quickly began to inundate our bushes. We frequently had to pause to recage plants and curb honey bee visitation. It was suspected that the uncaged pollinizer bushes were seriously depleted of nectar by mid-afternoon and honey bees probably found our potted plants to be more rewarding. We categorized bee foraging behavior throughout the observation periods into seven recognizable sequences or "treatment classes" for each flower: 1) virgin, unvisited *V. ashei* flowers (V); 2) ≥1 male *X. virginica* robbery visit (X); the number of slits was recorded for each robbed flower; 3) a single legitimate visit by *A. mellifera* (A_L); 4, a single *A. mellifera* robbing visit after a flower was slit 1–4 times by *X. virginica* (X, A_R); 5) >1 legitimate or illegitimate *A. mellifera* visit for ≈1 h ($A_{1\ h}$); 6) unrestricted bee visitation (open pollination) for 24 h ($O_{24\ h}$); these flowers were from uncaged plants; and 7) one legitimate visit from a female southeastern blueberry bee (H). It was important to use this effective bee as a benchmark pollinator because it is recognized as a superior blueberry pollinator (Cane and Payne 1988). Therefore, stigmatic loads accomplished by robbers can be compared with stigmas receiving no visits, multiple visits, and visits from native *H. laboriosa*.

Blueberry pollen tetrads were too small (≈30 μm) to be counted in situ; therefore, we harvested stigmas for microscopic examination. Flowers were removed immediately from the plant after a bee completed a visit sequence and departed. Flowers were detached from the raceme at the pedicel, inverted (i.e., pistils turned upward), and placed singly into wells of a plastic 96-well microtiter tray. Flowers were arranged by treatment on the trays and returned to the laboratory within 1 h. Protruding stigmas and 2 to 3 mm of the style were severed with forceps, mounted on glass slides, and stained for 24 h by using acid fuchsin stain in lactophenol. A plastic coverslip was applied to the stain droplet with reasonable force to smear stigmatic tissue and more evenly disperse pollen tetrads (Kearns and Inouye 1993). Pollen tetrads were examined under a microscope at 40× magnification and counted to generate stigmatic pollen loads. Only pollen grains found in the exudate were counted as having been legitimately delivered by a bee. We did not count any pollen tetrads attached to the style or deposited beneath the stigmatic flange, because these were likely self-pollen tetrads prematurely ejected from
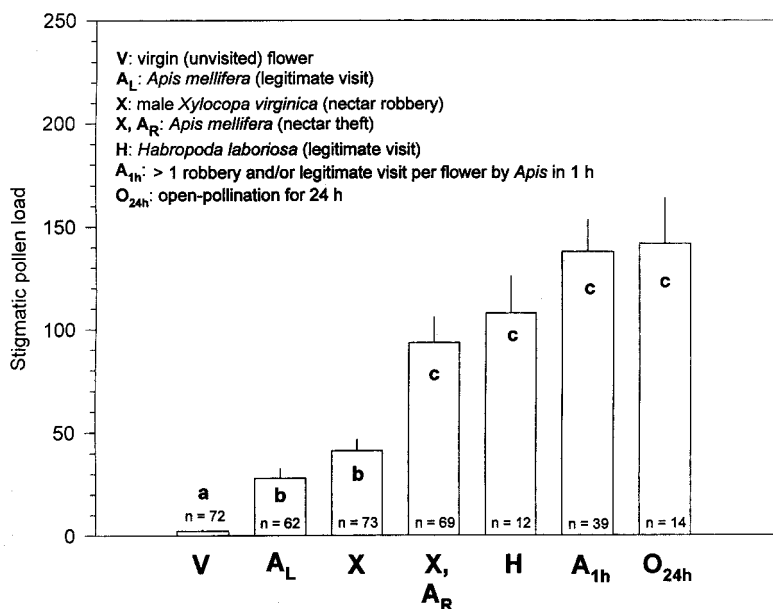
Fig. 1. Mean (+ SE on vertical bar) stigmatic pollen loading of *Vaccinium* pollen tetrads for *V. ashei* flowers receiving specific visitation sequences by *X. virginica* males, *A. mellifera*, and *H. laboriosa*. The number at the foot of each bar indicates sample size. Larger lowercase letters near the bars that are the same indicate means that are not significantly different at $P \leq 0.05$ using Tukey's HSD.

anthers during a bee's visit. Unvisited controls (V) showed that simply agitating flowers (by wind, removing plants from cages, and placing them in the field) contributed negligibly to stigmatic loading (Figs. 1 and 2).

Field Study. *X. virginica* robbery rates at *V. ashei* inflorescences and resulting fruit sets were monitored for 'Climax' and 'Tifblue' in 10 commercial fields (mean planting area 4.0 ha; range 0.4–30.0 ha) in Louisiana during March and April 2003. Terminal shoots with clusters of open flowers were enclosed in fine-mesh bags ($\approx$12 by 12 cm, mesh size $\approx$0.5 mm) closed with drawstrings. Bags were used to prevent any additional robbery and visitation once we had already determined the frequency of corolla slitting by *X. virginica*. Approximately 200 flowers were examined for each cultivar at each site with the exceptions that 'Tifblue' did not occur at one site, and data were lost from one 'Tifblue' plant at another site. Approximately 50 flowers in a total of four to six bags were enclosed on each of four plants to achieve this sample. The number of slit corollas was recorded for each group of bagged flowers to establish the robbery rate for each bush and cultivar at the site. The percentage of green fruit set by flowers was measured 8–14 d after bagging on 'Climax' and 22–26 d after bagging on 'Tifblue'.

Data Analysis. Normality was substantially improved for stigmatic loading data with the log $(Y + 1)$ transformation (Kolmogorov–Smirnov D-test and normal-probability plot comparisons, PROC UNIVARIATE, SAS Institute 1985). There were no significant differences in stigmatic loads between cultivars

($F = 2.20$; df $= 2, 331$; $P > 0.1$), so data for all cultivars were pooled before analysis to increase sample size. Subsequently, one-way analysis of variance (PROC GLM, SAS Institute 1985) tested for differences in stigmatic loads among the seven flower visitation se-
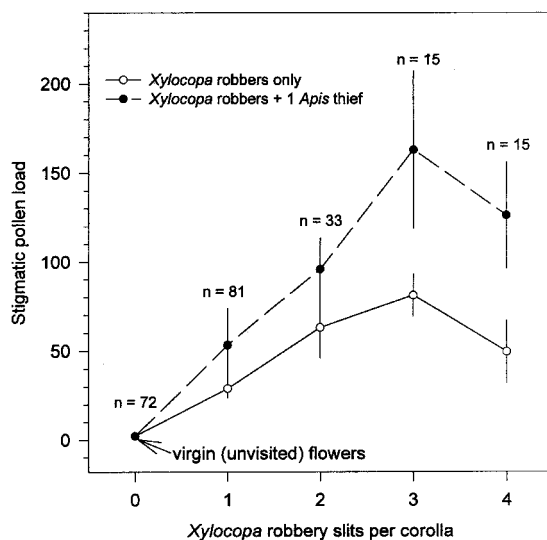

Fig. 2. Relationships between the number of robbery slits per corolla and stigmatic pollen loads generated by *X. virginica* males (open circles) and nectar theft by *A. mellifera* (*X. virginica* + 1 *A. mellifera* visit, dark circles). Symbols represent mean ($\pm$ SE on vertical bar) and sample sizes are provided for each robbery level.

Table 1. Pearson rank correlations between the percentages of flowers robbed and percentages of fruit set for (Climax) and (Tifblue) rabbiteye blueberry cultivated on 10 farms throughout Louisiana

Variable	Mean	SD	Min	Max	n (plants)	Pearson's rank correlation	
						r	P > r
% Robbery (Climax)	61	29	8	98	32	−0.015	0.933
% Fruit set (Climax)	92	9	68	100	32		
% Robbery (Tifblue)	41	23	9	81	35	−0.035	0.841
% Fruit set (Tifblue)	58	16	21	92	35		

Observations of fruit set and robbery rates for each bagged plant ($n \approx 50$ flowers per plant) were used in the correlation analyses.

quences. Residual mean square error was used in calculating F ratios. Mean separation was accomplished with Tukey's honestly significant difference (HSD) test with a critical $P = 0.05$ (PROC GLM, SAS Institute 1985). Analysis of covariance tested the effects of robbery intensity (i.e., the number of slits a corolla received) on stigmatic loading achieved by carpenter bee visits and subsequent honey bee visits. Polynomial contrasts identified possible linear, quadratic, and cubic trends in the relationship between the five levels of robbery (covariate; Fig. 2) and stigmatic pollen loading.

For field data, robbery rates and fruit set were calculated on a per plant basis for each cultivar. These data were subjected to Pearson's correlation analysis (PROC CORR, SAS Institute 1985). Negative correlations between robbery and fruit set would occur if robbery is deleterious; positive or no correlation signifies no adverse effects due to robbery. Green fruit sets, which normally range from 60 to 80% for *V. ashei* (R.G.D. and B.J.S., unpublished data), were abnormally very low (2 and 31%) on 'Climax' bushes in two fields; these data were excluded from analyses.

Results

The absence of bee visitation resulted in substantially less pollen deposition than all other bee visitation treatments (Fig. 1; $F = 57.55$; df = 6, 331; $P \leq 0.0001$). Bee visits at the Mississippi site resulted in essentially 98 to 99% pure *Vaccinium* pollen being transferred to stigmas. Legitimate flower visitation by carpenter bee males was rarely observed ($n = 2$ of 144 visits). However, nectar theft by carpenter bees still contributed ≈40 tetrads per stigma, an amount 20 times higher than if a flower went unvisited (Fig. 1; X versus V; $P \leq 0.05$; Tukey's HSD). Nectar robbing *X. virginica* and legitimate *A. mellifera* foragers transferred approximately the same number of tetrads (Fig. 1; A_L versus X; $P > 0.05$). Each single sequence of nectar robbery by *X. virginica* followed by a *A. mellifera* robber was approximately additive and almost doubled pollen loads on the stigma (Figs. 1 and 2). Thus, legitimate and illegitimate visits by *A. mellifera* apparently deposited similar amounts of pollen on rabbiteye blueberry flowers (Fig. 1; A_L versus X, $A_R - X$; $P \leq 0.05$). Multiple visits by *X. virginica*, indicated by the number of robbery slits, proportionally enhanced stigmatic pollen loads (Fig. 2; $F = 33.53$;

df = 1, 205; $P \leq 0.0001$), and also enhanced the pollination efficacy of subsequent *A. mellifera* robbers (Fig. 2; regression slope comparison: $t = 2.87$; df = 1, 139; $P \leq 0.005$). There were significant quadratic trends in stigmatic loading across the five different robbery levels (Fig. 2; $P \leq 0.0001$), and corollas with four robbery slits were associated with a slight, but noticeable reduction in the pollination efficacies of male *X. virginica* and *A. mellifera* workers (Fig. 2).

Pollination efficacy was higher for *H. laboriosa* than it was for *A. mellifera* and *X. virginica* (Fig. 1; $P \leq 0.05$). Southeastern blueberry bees always visited rabbiteye blueberry flowers legitimately via the corolla opening. A single *A. mellifera* robber following a *X. virginica* (X, A_R) transferred as much pollen as was received by open-pollinated flowers for 24 h $(O_{24 h})$ and single visits by *H. laboriosa* (Fig. 1; $P > 0.05$).

There were no significant correlations (negative or positive) between *X. virginica* robbery rate and *V. ashei* fruit set (Table 1) under orchard conditions where wild bees also had access to robbed flowers. Robbery rates at the time of counting were extremely variable, ranging from 8 to 98% (mean 61%) for 'Climax'. 'Tifblue' had lower rates of robbery and reduced levels of fruit set (Table 1). There was a narrower range for percentage fruit set than there was for floral robbery rate (Table 1).

Discussion

Rabbiteye blueberries produce flowers that are physically and genetically self-incompatible (Dorr and Martin 1966, Marucci 1967, Cane 1993, Free 1993, Sampson and Cane 2000). Few or no compatible pollen tetrads can reach stigmas without being vectored by a pollinating insect. Consequently, floral visits by male carpenter bees and honey bees might achieve levels of cross-pollination beneficial to the plant, despite the popular idea that primary and secondary robbery circumvents blueberry pollination. It has been demonstrated experimentally that encounters with robbing carpenter bees are not always deleterious to plant pollination. Robbing *X. virginica* make contact with receptive stigmas of ocotillo, *Fouquieria splendens* Engelm., and Virginia bluebell, *Mertensia virginica* (L.) Pers. flowers, and repeated robbery further enhances pollination, fruit set, and seed production (Waser 1979, Scott 1989, Enz 2001).

Pollination responses similar to those of ocotillo and bluebells may occur for blueberry flowers experiencing more moderate levels of nectar robbery. Our data show that males of *X. virginica* that visited virgin *V. ashei* flowers transferred an average of 25 tetrads to each flower's stigma and that a similar level was added to the stigma with each succeeding visit by a male bee. Multiple visits by carpenter bees achieved higher stigmatic loads. It also seemed that robbing honey bees and carpenter bees were equally effective pollinators during their first visit to *V. ashei* flowers and that repeated slitting of corollas provided a small boost to pollination by attracting honey bee robbers. Multiply slit blooms might invite greater probing by honey bees thereby prolonging floral handling and increasing the likelihood of stigmatic contact by the bee. Greater visitation, stigmatic contact, and pollen loading increases fruit set for other plants that are related to *V. ashei*, e.g., southern highbush blueberry (Danka et al. 1993) and cranberry *Vaccinium macrocarpon* Ait (Cane and Schiffhauer 2001).

There is still a possibility that fruit sets may differ between slit and unslit blooms due to robbers differing in the proportions of viable tetrads they deliver. However, this is less of a concern in these present studies, because varieties of *V. ashei* were visited by bees that deposited essentially pure pollen loads (i.e., 98 to 99% *Vaccinium* tetrads). Our pollinizer arrangement should also minimize geitonogamy, and analyses of *V. ashei* fruit set did not detect any obvious adverse effects associated with *Xylocopa* robbery in commercial blueberry fields.

Bees that collect nectar and avoid pollen are generally less efficient blueberry pollinators (Javorek et al. 2002, Sampson and Spiers 2002). This is a potential challenge for most southern blueberry producers faced with a situation where nectar foraging bees are the prevailing crop pollinators. Our data show that greater rates of nectar foraging stimulated by robbery incrementally enhances stigmatic loading. Often the levels of stigmatic loading that nectaring *X. virginica* and *A. mellifera* attained together were equal to or in excess of those achieved by pollen-foraging females of *H. laboriosa*, the most effective blueberry pollinator known in the southeastern United States (Cane and Payne 1988, 1990, 1993; Sampson and Cane 2000). Because robbing and legitimate honey bee foragers were equivalent pollinators based on their average stigmatic loads, commercially acceptable levels of *V. ashei* pollination are possible with some degree of floral robbery.

An argument can be made that excessive robbery might still deter future visitation by other pollinators, affect the quality of the delivered pollen, or damage flowers in a way that later impedes fertilization (Utelli 1998) because we did not track fruit and seed set for robbed flowers. Excessive robbery of *V. ashei* flowers only slightly reduced stigmatic loading for both nectar robbers and thieves at our blueberry flowers. Additionally, farm-wide robbery damage assessed in our second study did not seem to reduce fruit set for two *V. ashei* cultivars, even though about one-half of the flowers tagged were slit. These data are consistent with the observations of Delaplane and Dedej (2001) who found doubling carpenter bee densities inside small pollinator enclosures stocked with honey bees did not reduce *V. ashei* fruit set. However, flowers did receive slightly poorer pollination at higher robbery rates, based on the number of mature seeds sired per fruit.

Our study shows for the first time that male carpenter bees and worker honey bees can transfer blueberry pollen during floral robbery. Increased robbery enhances stigmatic loading at rabbiteye blueberries, thereby increasing the chances of successful pollination and fruit set. Considering the greater abundance of honey bees and the intensity of visitation that they show toward blueberry flowers, facts revealed in this study are strong support for the use of the honey bee as a viable blueberry pollinator. The presence of *X. virginica* robbers in combination with honey bees may actually be beneficial to *V. ashei* cross-pollination. Easy access to floral nectaries that robbery holes provide to honey bees may serve as a positive foraging stimulus.

Acknowledgments

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